

MORPHOMETRIC DIFFERENTIATION AMONG
WEST AFRICAN POPULATIONS OF THE RODENT
GENUS *DASYMYS* (MUROIDEA: MURINAE),
AND ITS TAXONOMIC IMPLICATIONS

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Abstract.—Craniodental variation among West African samples of *Dasymys* is reassessed based on the larger museum series now available. Two morphological kinds can be discerned in this region and are referable to the locally available epithets *Dasymys rufulus* Miller (1900), described from Mount Coffee, Liberia, and *Dasymys foxi* Thomas (1912), named from Panyam, Nigeria. The degree of craniodental differentiation between these two phenotypes matches that documented for other congeneric pairs of murid rodent species inhabiting parts of West Africa. *Dasymys rufulus* differs from *D. foxi* by its overall smaller size, especially as observed in its smaller, narrower cranium and less robust molars. In West Africa, samples of *D. rufulus* are broadly distributed from east of the Niger River, Nigeria, west to northern Sierra Leone; whereas, the known examples of *D. foxi* are restricted to the Jos Plateau in Nigeria. *Dasymys rufulus* and *D. foxi* are provisionally accorded specific status until taxonomic studies of *Dasymys* populations from other parts of Africa are undertaken to determine their relationships and distributional limits. It is doubtful that either form, but especially *D. rufulus*, is synonymous with *D. nudipes* or *D. incomtus*.

Shaggy-furred or marsh rats of the genus *Dasymys* are broadly if intermittently distributed over much of Africa south of the Sahara Desert, inhabiting a variety of wetland areas with thick ground cover. Current classifications recognize a single species, *Dasymys incomtus* (Sundevall, 1847), throughout this broad range (Misonne 1974, Honacki et al. 1982, Corbet & Hill 1986). The genus has not always been viewed as monotypic, for 13 of the 20 species-group taxa associated with *Dasymys* have been named as species. As of 1939, Allen listed 10 species, four of them containing from two to four subspecies.

The current perception of species diversity in *Dasymys* originated with Ellerman's (1941) treatment of the genus. Ellerman (1941:121) regarded all named forms, except *orthos* Heller (1911) which he did not examine, as races of *D. incomtus*: "It ap-

pears very unlikely that there is more than one species of this genus." His conviction in this regard may have been influenced by Osgood's (1936:256) earlier observation that "Both external and cranial characters in this genus are elusive and the range of variation throughout is comparatively slight," which he offered in the description of *D. incomtus griseifrons*. Except for the occasional retention of *D. nudipes* as a species (Roberts 1951, Crawford-Cabral 1983), subsequent classifications and regional catalogues have uniformly acknowledged the one species *D. incomtus* (for example, Ellerman et al. 1953, Hanney 1965, Rosevear 1969, Delany 1975, De Graff 1981, Meester et al. 1986, Hapold 1987). A notable omission in arriving at the current species arrangement of shaggy-furred rats has been the presentation of data supportive of these taxonomic changes. The basis for recognition of a single species

has hinged on Ellerman's surmise that "it appears very unlikely" that more than one exists.

The present study contributes distributional and morphological information that bears on the status of *Dasymys* populations inhabiting portions of West Africa, namely from Nigeria west to Sierra Leone. Compared to the number of forms described from eastern and southern Africa, the taxonomy of shaggy-furred rats is less problematic in West Africa, where only two forms have been described: *Dasymys rufulus* Miller (1900) from Mount Coffee, Liberia, and *Dasymys foxi* Thomas (1912) from Pan-yam, on the Jos Plateau, Nigeria. Clarification of patterns of morphological variation on a regional basis, set within the context of local taxonomic designations, marks a necessary step toward refining the species taxonomy of *Dasymys* as a whole and gaining insight into its historical zoogeography.

Like other forms of *Dasymys*, Miller's *rufulus* and Thomas' *foxi* were viewed as subspecies of *D. incommutus* by Ellerman (1941), an arrangement which has persisted to the present day (Rosevear 1969, Misonne 1974, Happold 1987). Rosevear (1969:311) even questioned the validity of maintaining any formal racial division among West African populations: "... the differences in size between this race [that is, *rufulus*] and *foxi* are really very slight and it is open to some doubt whether the distinction can be retained." Happold (1987:132) formed a similar impression based on his review of Nigerian samples, noting that, in general, the smaller *rufulus* occurs in southern localities and the larger *foxi* in northern ones, but that "... the subspecific distinction may not be valid." These assessments deserve review based upon the larger museum series of West African *Dasymys* now available.

Materials and Methods

Approximately 300 specimens, consisting of conventional study skins with asso-

ciated skulls, were examined (see Taxonomic Summary) from the following collections, their acronyms listed in parentheses: American Museum of Natural History, New York City (AMNH); Museum of Comparative Zoology, Harvard University, Cambridge (MCZ); and the U.S. National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM).

Preparation of the distribution map was based on locality information and geographical coordinates basically as given by collectors on specimen tags. We also consulted the gazetteers provided by Davis & Misonne (1964), Rosevear (1965) and Happold (1987), to verify the plotting of these sites and to obtain geographical coordinates not listed by collectors.

Several dimensions of the skin and skull were recorded in millimeters (mm) to characterize the morphology of the samples. Total length, tail length (TL), and hindfoot length (HFL) were extracted to the nearest whole mm from the skin tag, as was field weight to the nearest whole gram (gm). Length of the head and body (HBL) was obtained by subtracting the tail from total length. Fourteen cranial and two dental measurements were taken to the nearest 0.01 mm by means of hand-held digital calipers accurate to 0.02 mm. These measurements, and their abbreviations as used herein, include: occipitonasal length (ONL); greatest zygomatic breadth (ZB); breadth of the braincase (BBC); least interorbital breadth (IOB); length of the rostrum (LR); breadth of the rostrum (BR); postpalatal length (PPL); length of the bony palate (LBP); length of the incisive foramen (LIF); length of the diastema (LD); breadth of the bony palate across the upper first molars (BM1s); breadth of the zygomatic plate (BZP); length of the auditory bullae (LAB); breadth across the exoccipital condyles (BEC); crown length of the maxillary toothrow (LM1-3); and width of the upper first molar (WM1). The limits of most of these dimensions on the murine skull are defined and illustrated by Musser (1979).

Recording of measurements was limited to animals judged to be adult based on the possession of fully erupted third molars and adult pelage. "Adult" animals were further segregated into crude age classes based on upper molar wear as follows.

Young adult.—Tricuspid arrangement of first and second chevrons of M1–2 well defined, the enamel borders of the medial (t1 and t3) and lateral (t3 and t6) cusps deeply constricted and contiguous or virtually so; dentinal lakes of chevrons thus narrow and discontinuous transversely or nearly so; M3 erupted and slightly worn; t1s on M2–3 wholly isolated from enamel borders of second chevron; transverse enamel valleys between chevrons deep and extend across the width of the molar.

Full adult.—Enamel indentations of the medial and lateral cusps on chevrons of M1–2 not in contact, their dentin basins broader and continuous across the width of the tooth; enamel, less often the dentin, of t1s on M2–3 connected to that of the second chevron (anterior border of t5).

Old adult.—Occlusal wear heavy such that the dentin of chevrons, particularly the middle one and t8, cross-connected at their medial and lateral edges; enamel valleys separating chevrons appear as islands surrounded by dentinal basins.

Although the above data were recorded for all specimens examined, the multivariate analyses were applied to the larger population samples with the highest incidence of intact crania. These are:

OTU G3.—Ghana, Pulima, $n = 37$.

OTU I1.—Ivory Coast, Kong, $n = 10$.

OTU I2.—Ivory Coast, Sienso, $n = 15$.

OTU L1.—Liberia, Mount Coffee, $n = 5$ (type series of *rufulus*).

OTU N4.—Nigeria, Dada, $n = 24$.

OTU N10.—Nigeria, Jos Plateau, Panyam Fish Farm, $n = 43$ (near type locality of *foxi*).

OTU T3.—Togo, Padori, $n = 11$.

Standard descriptive statistics (mean, range, standard deviation) were derived for the OTUs (see Appendix 1). One-way anal-

yses of variances were applied to the three largest OTUs (G3, N4, and N10) to assess the effect of gender on the variation of the 16 craniodental variables. Principal components were extracted from a variance-covariance matrix and computed using the craniodental variables after transformation to their natural logarithms. Loadings are expressed as Pearson product-moment correlation coefficients of the principal components with the original cranial variables. All analytic procedures were carried out using Systat (Version 4.1, 1989), a series of statistical routines programmed for microcomputers.

Morphometric Results

Sexual dimorphism in cranial size is unappreciable within populations of *Dasymys*, a finding in agreement with biometric studies of other African murines (for example, Van der Straeten & Verheyen 1981, 1982; Carleton & Robbins 1985). Among the three largest population samples analyzed, only six cranial dimensions vary significantly with regard to gender (Table 1), with males larger in each instance, and each significant variable is unique to a particular sample. We attribute the sporadic occurrence of significant findings across the three samples to a combination of Type I sampling errors and unequal age representation among the sexes of each sample. For example, within the Panyam sample (N10), males are disproportionately represented in the adult (12 to 9) and old adult (2 to 0) age groups. As discussed below, age can contribute substantial intrapopulation variation. In view of the negligible or inconsistent effects, particularly with regard to the magnitude of interlocality differentiation, both sexes were included in the multivariate analyses.

With the large series available from near the type locality of *D. foxi*, populations in Nigeria have provided critical insight to the morphological differentiation among West African *Dasymys*. Thomas (1912) diagnosed *D. foxi* on the basis of its larger

Table 1.—*f* values from one-way anovas (effect = sex) of three population samples of West African *Dasymys*.

Cranial variables	Ghana: Pulima (14 ♂, 23 ♀)	Nigeria: Dada (8 ♂, 15 ♀)	Nigeria: Panyam (22 ♂, 16 ♀)
ONL	0.31	1.27	3.96
ZB	0.01	2.11	2.65
BBC	0.43	6.17*	1.54
IOB	5.70*	0.11	0.63
LR	0.52	0.06	3.70
BR	0.48	0.29	5.46*
PPL	0.54	0.49	2.47
LBP	0.10	0.62	6.83*
LIF	0.61	0.01	0.83
LD	0.70	0.63	3.17
LM1-3	1.69	2.06	0.01
WM1	0.13	0.84	0.06
BM1s	0.01	0.51	0.02
BZP	0.11	1.41	0.16
LAB	0.22	13.68**	0.42
BEC	0.61	2.83	11.62**

* = $P \leq 0.05$; ** = $P \leq 0.01$.

size, especially as observed in the length and breadth of the molar rows. Such differences were borne out in principal component analyses of the two largest Nigerian samples, Dada and Panyam Fish Farm, whose scores overlapped little in multivariate space (Fig. 1). The uniformly positive and high correlations of most craniodental variables with the first principal component suggest a general size factor (Table 2) and emphasize the overall larger size of the Panyam specimens. The dispersion of individuals along the second principal component reflects certain breadth measurements (BEC, IOB) and size of the molars (LM1-3, WM1), which again reflect the broader cranium and more robust molars recorded for the specimens from the vicinity of Panyam.

Some age-related size variation undoubtedly contributes to the elliptical spread observed for each population sample in the bivariate plot of the first two principal com-

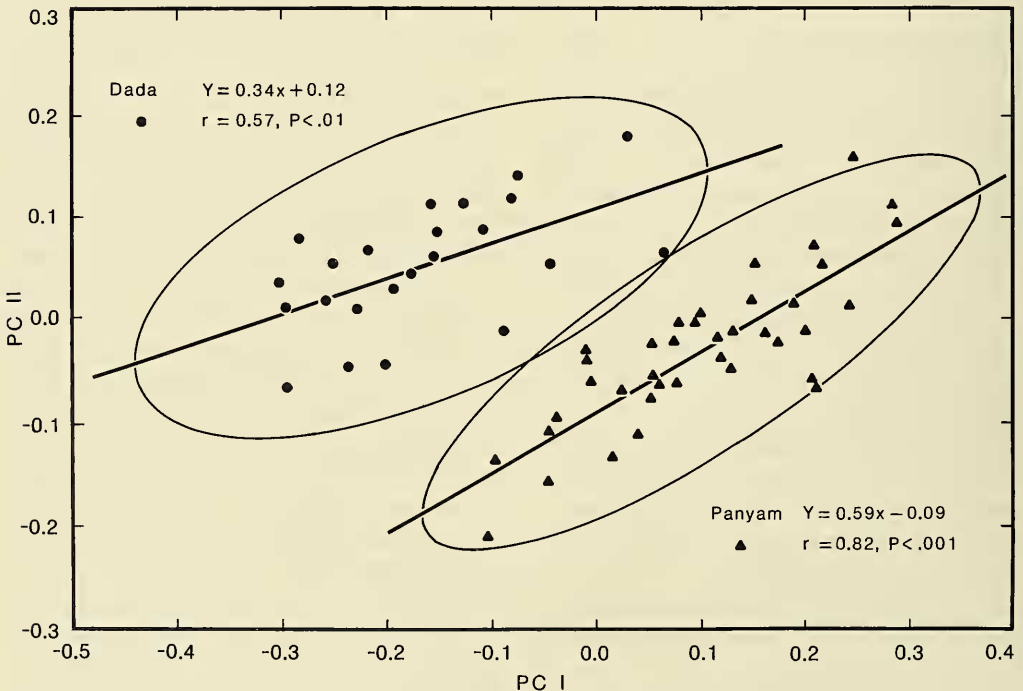


Fig. 1. Projection of individual specimen scores on the first two principal components for the two largest samples of Nigerian *Dasymys*, Dada ($n = 23$) and vicinity of Panyam ($n = 38$). Ellipses correspond to 95% confidence envelopes for scores of individuals within each sample. See Table 2.

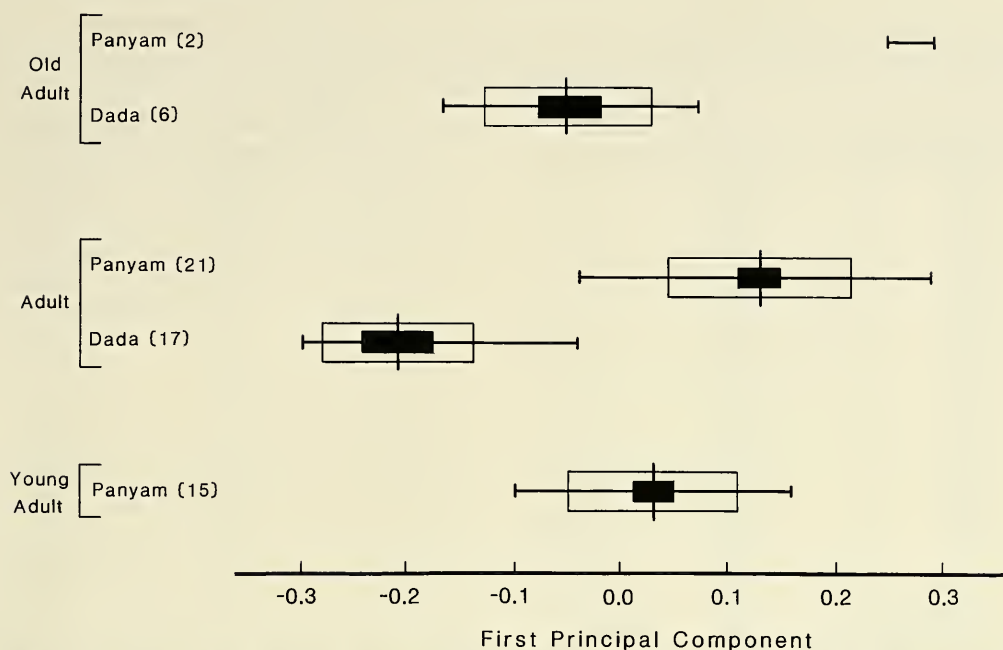


Fig. 2. Box plots of first principal component scores (see Fig. 1) of Dada and Panyam samples arranged by three adult age classes. Mean (vertical line), one standard error of the mean (closed rectangle), one standard deviation (open rectangle), and the range (horizontal line) are indicated.

ponents (Fig. 1). The range of factor scores viewed by age class suggests such an influence, especially for the first principal component (Fig. 2). Still, a marked separation between the Dada and Panyam samples is apparent for a given age class. The absence of specimens classified as young adults in the Dada sample probably accounts for its wider confidence ellipse as well as the marginally significant difference ($P = 0.052$) in the slopes of their regression equations.

Rotation (varimax procedure) of the principal components underscored the same disparity in cranial breadth (ZB, BBC, IOB, BEC) and molar size (LM1–3, WM1) between the Dada and Panyam samples, as well as in the LAB (Table 2). One-way analyses of variance, using locality as the category of effect, generally corroborated the higher variability of these dimensions, with WM1, BEC, and LM1–3 exhibiting the largest f values, respectively (Table 2). Although the principal component and anova

results are here reported only for the Dada and Panyam samples, all Nigerian specimens with intact skulls were subjected to the same analyses and revealed the same pattern of dual clouds of points. Specimens from the Jos Plateau (Panyam Fish Farm, 2 mi N Panyam, and Ugar Jabar), which represent Thomas' (1912) *D. foxi*, formed one of those constellations, whereas the other corresponded to specimens from all other localities in Nigeria (see Specimens Examined).

The distinctiveness of the animals from the vicinity of Panyam is still apparent in principal component analyses including samples from four other West African countries (Fig. 3). Again, overall larger size—in particular as expressed by the IOB, BEC, LAB, LM1–3, and WM1—contributed to the separation of this Nigerian sample from other West African *Dasymys* (Table 3). Confidence ellipses for the centroids of the latter populations, including the Dada sam-

Table 2.—Results of principal component analyses and one-way anovas (effect = locality) for Dada (*n* = 23) and Panyam (*n* = 38) samples of *Dasymys* (see text and Fig. 2).

Cranial variables	Unrotated		Rotated		<i>f</i> (locality) ¹
	PC I	PC II	PC I	PC II	
ONL	0.92	0.29	0.88	0.34	37.0
ZB	0.90	0.04	0.68	0.52	54.8
BBC	0.79	−0.21	0.45	0.65	59.8
IOB	0.52	−0.53	0.02	0.73	37.5
LR	0.79	0.44	0.84	0.14	15.8
BR	0.74	0.29	0.81	0.24	9.9
PPL	0.88	0.29	0.86	0.32	29.3
LBP	0.59	0.11	0.40	0.27	12.2
LIF	0.71	0.29	0.76	0.22	14.9
LD	0.81	0.47	0.89	0.13	12.6
LM1–3	0.76	−0.46	0.25	0.83	119.7
WM1	0.75	−0.61	0.15	0.94	273.7
BM1s	0.84	0.04	0.51	0.47	27.7
BZP	0.77	0.25	0.41	0.24	20.2
LAB	0.79	−0.27	0.47	0.71	76.0
BEC	0.77	−0.43	0.35	0.82	194.5
Eigenvalue	0.027	0.006	0.016	0.014	
% Variance	60.4	14.0	34.1	31.2	

¹ All *f* values significant at *P* ≤ 0.01.

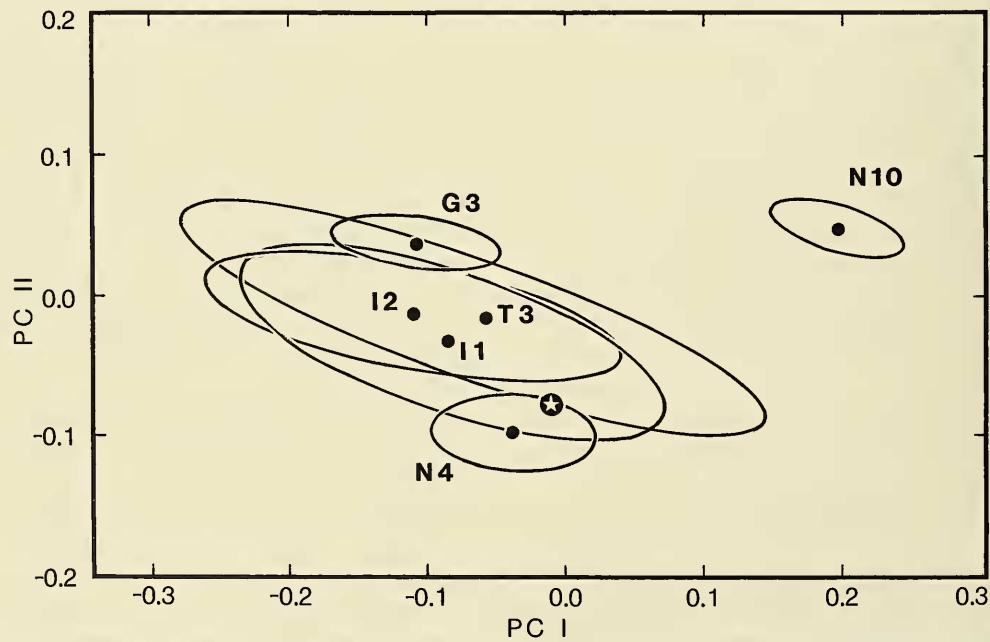


Fig. 3. Projection of group centroids on the first two principal components for six largest samples of West African *Dasymys* (see Table 3; sample codes and sizes are given in Materials and Methods). Ellipses correspond to 95% confidence limits of a group's centroid. Enclosed star represents the holotype of *Dasymys rufulus* Miller (1900).

ple, were broadly congruent and circumscribed the data point that represents the type specimen (USNM 83844) of Miller's (1900) *D. rufulus*. Although we did not personally examine the type material of *D. foxi*, the cranial measurements of the holotype (BMNH 12.4.3.15 from Panyam) supplied by Dr. Erik Van der Straeten clearly depict a robust skull that fits with the USNM series from the Jos Plateau.

Discussion

Several of the common names applied to *Dasymys*—namely, “marsh,” “swamp,” or “water” rats—underscore the regular association of these rodents with various kinds of wetland environments. Typical habitat references include stream and river banks, marshy areas with reed beds, swampy edges along rivers, lush grass covering moist ground, matted semi-aquatic grasses and sedges, wetter parts of floodplains, and highland bogs (Rosevear 1969, Smithers 1971, Sheppe 1972, Kingdon 1974). In addition to preferring generally wet conditions, the presence of dense ground cover appears critical to their ecological occurrence in affording protected runways and nesting sites. Their diet is thought to consist principally of green vegetable matter, yet some insects remains have been identified in stomach contents (Hanney 1965, Smithers 1971, Coe 1975). Shaggy-furred rats appear to be mostly terrestrial, although semi-aquatic habits have been noted, and their activity has been described as principally nocturnal but to a limited extent diurnal (Thomas 1912, Roberts 1951, Smithers 1971, De Graaff 1981).

Knowledge of the life history and ecology of *Dasymys*, however, remains sketchy and stems largely from trapping experiences related in faunal accounts and from collectors' notations on specimen tags. Thorough field studies on the biology of this genus have yet to be conducted, a situation which leaves unanswered whether some of the apparent

Table 3.—Results of principal component analysis using six largest OTUs of *Dasymys* (*n* = 130) (see text and Fig. 3).

Cranial variables	PC I	PC II	PC III
ONL	0.96	−0.18	0.09
ZB	0.89	0.03	0.05
BBC	0.76	0.19	0.16
IOB	0.30	0.58	0.16
LR	0.87	−0.33	0.08
BR	0.81	−0.24	0.13
PPL	0.92	−0.09	0.05
LBP	0.68	−0.14	−0.17
LIF	0.80	−0.15	0.22
LD	0.91	−0.27	0.07
LM1–3	0.61	0.60	0.17
WM1	0.51	0.74	0.16
BM1s	0.87	0.05	−0.01
BZP	0.78	0.16	−0.59
LAB	0.71	0.41	0.12
BEC	0.68	0.37	0.16
Eigenvalue	0.033	0.005	0.003
% Variance	63.5	10.4	5.9

variation in habitat and habit reflects populational or specific differences.

In West Africa, the pattern of morphological variation supports the existence of two separate species, to which the closest regional epithets *Dasymys rufulus* Miller (1900) and *Dasymys foxi* Thomas (1912) apply. The marked discrimination between these two sets of populations clearly disputes the notions that the traits of *rufulus* and *foxi* are insufficiently marked for even subspecific recognition or that they intergrade imperceptibly in size along a north-south cline (Rosevear 1969, Happold 1987). Instead, the craniodental differentiation observed between populations of each resembles that demonstrated for other pairs of congeneric species inhabiting portions of West Africa—for example those of *Hybomys*, *Lemniscomys*, *Malacomys*, and *Praomys* (Van der Straeten & Verheyen 1978, 1979, 1981, 1982; Carleton & Robbins 1985).

How these two species in West Africa relate to forms of *Dasymys* described from central, eastern, and southern Africa will

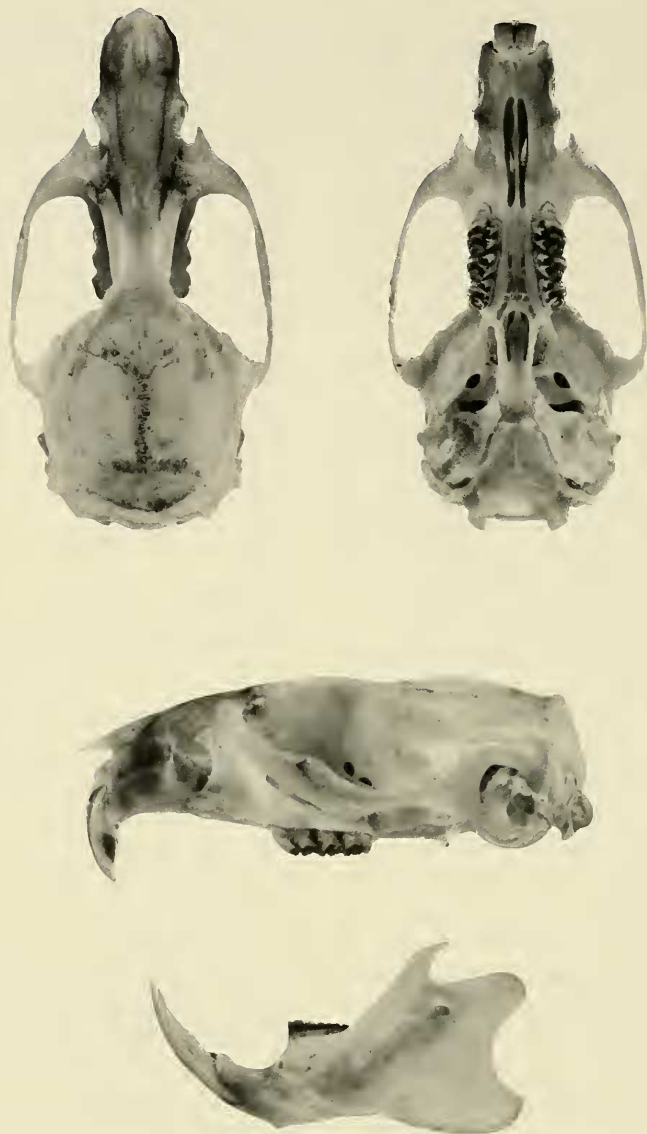


Fig. 4. Views of the cranium and mandible of an adult male *Dasymys foxi* (USNM 403644) from the vicinity of Panyam, Nigeria. Approximately $\times 1.75$.

require careful revisionary attention to the entire genus, which is beyond the scope of our paper. The primary descriptive literature on *Dasymys* lends few clues.

Miller (1900) contrasted his new species *Dasymys rufulus* to *D. bentleyae* and *D. incommutus*, but had at hand for examination only a single specimen of the latter (probably USNM 101884 from Port Natal, South

Africa). His enumeration of the differences between *D. rufulus* and *D. incommutus* is apt and emphasized the generally smaller size and more rufous pelage of the former relative to the larger skull, robust molars, and dark-toned pelage of the latter. These morphological contrasts are apparent in more recently collected examples of *D. incommutus* available to us from South Africa and Zim-

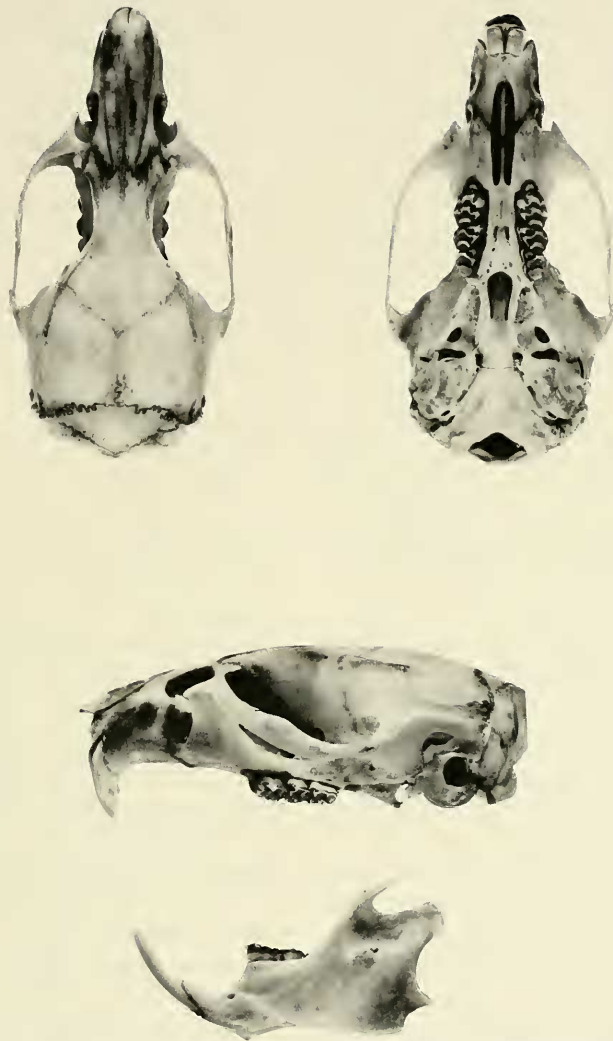


Fig. 5. Views of the cranium and mandible of an adult male *Dasymys rufulus* (USNM 83901) from Mount Coffee, Liberia. Approximately $\times 1.75$.

babwe. The eastern distributional limits of *rufulus* are uncertain; examples that we have seen from Cameroon (AMNH specimens from Tongo and Ndokayo) are referable to *rufulus*.

In his description of *Dasymys foxi*, Thomas (1912) had available for examination examples of *D. rufulus*, as well as specimens of *Dasymys* from other regions of Africa contained in the British Museum (Natural History). With only passing mention, he dismissed Miller's (1900) *D. rufulus*

as a close relative of *D. foxi*, based principally on the former's smaller molar rows, and instead focussed his comparisons to *D. medius* from central Africa.

Our principal component analyses corroborate Thomas' (1912) emphasis of molar size as a cardinal trait for distinguishing *D. foxi* from *D. rufulus*. The distinction rests not only with the greater length of the tooth-rows in *D. foxi* but also with their greater width (Tables 2, 3; Appendix 1). Breadth measurements across the zygoma and

braincase contribute substantially to the robust appearance of the skull of *D. foxi* versus that of *D. rufulus* (Figs. 4, 5), in general relatively more so than length variables (Table 2), although specimens of *D. foxi* do average larger in most cranial dimensions (Appendix 1). Field weights and external measurements of the skin similarly reflect the larger size of *D. foxi*, but overlap in ranges is appreciable (Appendix 1). Examples of *D. foxi* and *D. rufulus* are practically inseparable on the basis of pelage coloration: both exhibit a grayish to reddish brown dorsum and a light to dark gray venter with varying concentrations of a creamy-buff wash. Red tones seem more predominant in the dorsum of *D. rufulus* and gray in *D. foxi*, but this impression is undermined by the range of chromatic variation observed within series of each form.

We have not yet examined series of *D. medius* to form an opinion on its degree of similarity of *D. foxi*. In external and cranial size, however, specimens of *D. foxi* closely resemble those of *D. incomtus*, as known to us from several localities in South Africa and Zimbabwe. The agreement is particularly strong in their possession of heavily constructed, long tooththrows. Like *D. rufulus* the pelage color of *D. foxi* contrasts with the darker, grayish-black upper parts typical of *D. incomtus*. Moreover, the texture of its fur seems finer relative to both *D. foxi* and *D. rufulus*. The taxonomic significance of these pelage differences must await rigorous evaluation of variation using large series of *D. incomtus* and determination of its relationship with forms described from eastern and central Africa.

Miller (1900) erred in reporting five plantar pads as characteristic of *D. rufulus*. A sixth pad, the hypothenar, is present and, although small, is clearly discernable on the dried hind feet of most specimens comprising his type series. A total of six plantar pads also appears characteristic of *D. foxi* and of most other *Dasymys* from central, eastern, and southern Africa, which repre-

sent a variety of taxa including *incomtus* proper. Only examples of *D. nudipes* seem to typically lack a sixth pad (Hill & Carter 1941, Crawford-Cabral 1983), but we have examined too few specimens of this taxon to judge the constancy of the trait. In other features as well—more brightly colored dorsal and ventral pelage, large size (hind foot length typically 38 to 42 mm), and the usual presence of a tiny t3 on the upper second molar—*nudipes* represents a well-marked form that probably warrants specific status (also see Crawford-Cabral 1983 and Crawford-Cabral & Pacheco 1989).

Available data on chromosomal variation in the genus *Dasymys* is limited to standard karyotypic preparations. Matthey (1958) reported a diploid number of 38, with four pairs of biarmed autosomes, for a sample (number of individuals unknown) of *Dasymys* from Ivory Coast. Later, Tranier & Gautun (1979) obtained a similar figure for Ivory Coast *Dasymys*, $2N = 36$ with six pairs of metacentrics and submetacentrics based on two males. Both records are presumably referable to *D. rufulus*, but the variation implied by these studies should be reconfirmed using larger samples of fresh material. The one karyotypic example from eastern Africa, a single male from Burundi, exhibited a $2N = 40$, with six pairs of biarmed autosomes (Maddalena et al. 1989). The authors provisionally identified their specimen as *D. incomtus* but stressed the lack of chromosomal data based on true *incomtus* from South Africa. Although these studies suggest the potential value of karyotypic information in *Dasymys* systematics, the evidence is, as yet, too fragmentary to offer insight on species boundaries.

Unlike some other rodent species, samples of *Dasymys* from West Africa are not restricted to a particular faunal region or biome. Instead their geographic distribution spans several major biotic realms, including (per Delany & Happold 1979) lowland rain forest, Guinea savanna, and Sudan savanna (Fig. 6). Moist living conditions

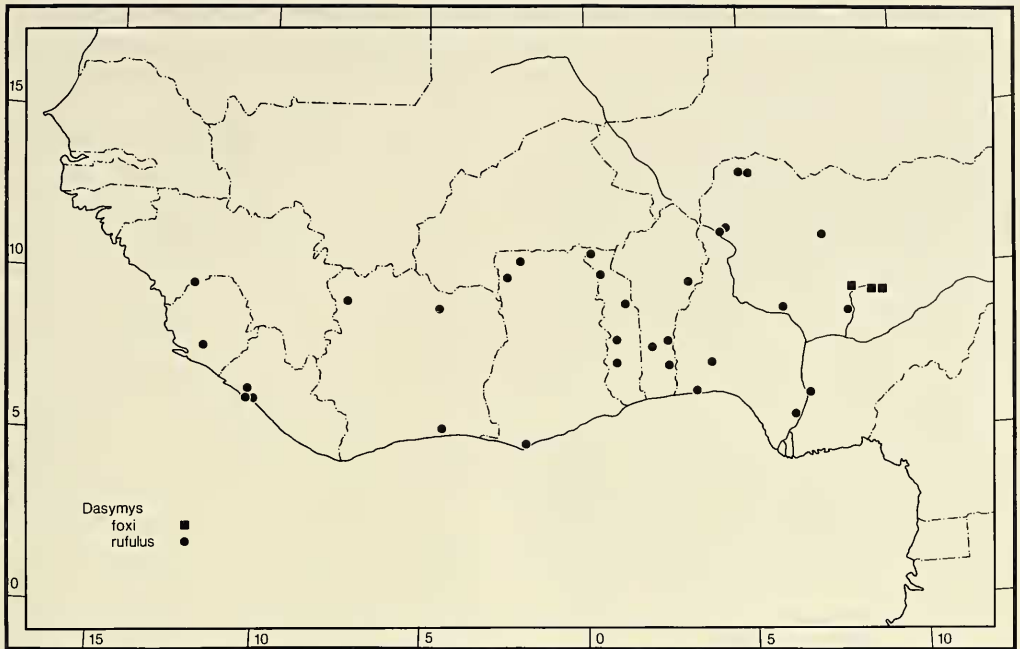


Fig. 6. Distribution map of West African *Dasymys* illustrating collecting localities reported herein (see Taxonomic Summary).

combined with dense ground cover, such as afforded by palustrine and riverine microhabitats within these vegetational zones, appear to be the critical factors that correspond to the presence of *Dasymys*, more so than the prevailing climatic, edaphic, and floristic features that typify these biomes. The inherently patchy nature of such wetland environments may account for the interrupted distribution among *Dasymys* populations. Moreover, the potential for geographic isolation and genetic differentiation within this ecological setting stands at odds with the notion of a single, pandemic species of shaggy-furred rat occurring throughout much of subSaharan Africa as portrayed in current classifications (Misonne 1974, Honacki et al. 1982, Corbet & Hill 1986).

The West African distribution of the two kinds of *Dasymys* identified herein, however, does correspond to one prominent ecogeographic feature. The few localities known for *D. foxi* are limited to the Jos

Plateau, a highland mass in eastcentral Nigeria; whereas, populations of *D. rufulus* are widely documented across the entire region, from just east of the Niger River, Nigeria, west to northern Sierra Leone (Fig. 6). Isolated within northern Guinea savanna, the central plateau itself rises to 1000 meters, with isolated peaks reaching 1500 to 2000 m, and supports a predominantly grassland vegetation with extensive rocky outcrops and few trees. The Jos Plateau experiences a wetter and cooler climate compared to that of the surrounding Guinea savanna and harbors relictual stands of rain forest along its southern slope (Happold 1985). We have not detected any instance of sympatry, but the two forms occur in close proximity in the vicinity of the Mada River, along the western edge of the plateau. Distributional transects in this region, as well as the southern slopes, would be highly informative.

Within Nigeria, Happold (1985, 1987) listed six species of mammals as restricted to this highland area—three rodents (*Ta-*

terillus nigeriae, *Dendromys melanotis*, and *Cryptomys ochraceocinereus*), two bats (*Rhinolophus alticolus* and *Miniopterus inflatus*), and one artiodactyl (*Oreotragus oreotragus*). In view of this modest level of endemism and its distinctive bioclimatic features, Happold recognized the Jos Plateau as one of eight major faunal regions within the country. He further suggested that the Plateau and the Cameroon highlands, located 500 km to the east, share certain faunal similarities (without elaborating these in detail). *Dasymys foxi* may qualify as another mammalian species whose distribution in West Africa is localized to the Jos Plateau and whose nearest relatives occur far outside the region to the east. Such a viewpoint accords with Thomas' (1912) original comparisons of *foxi* and *medius*, a form described from Mount Ruwenzori in the Rift Valley system. Nevertheless, as cautioned by Happold (1985), the establishment of past biotic links between the Jos Plateau and other regions of Africa must await better documentation of the Plateau's mammalian fauna. Of equal importance are the basic needs for alpha-level revisionary studies of the mammals occurring there and for persuasive arguments of interspecific relationships.

In summary, populations of *Dasymys* inhabiting other parts of Africa also exhibit substantial morphological variation, much of it grossly apparent as large-bodied animals with robust skulls and molars versus those with smaller proportions. Thus, whether *rufulus* or *foxi*, or perhaps both names, will prove to be junior synonyms of species described from other regions is uncertain at this stage of our taxonomic understanding of the genus. Although inspection of additional museum material indicates the occurrence of large and small forms in other geographic areas, we doubt that only two species, separated principally on size, exist over the vast subSaharan region. As noted above, *D. nudipes* is appreciably differentiated from both *rufulus*

and *foxi*, as well as from *D. incomtus*. The greater taxonomic complexity of the genus is further suggested by the preliminary study of Crawford-Cabral and Pacheco (1989), who detected four distinctive forms (*nudipes*, *incomtus*, *bentleyae*, and *fuscus*) in southern Africa but formally recognized only *D. nudipes* as a separate species.

There is little evidence to indicate that *rufulus* will be found to intergrade with populations of *D. incomtus*. The possibility that *foxi* and *D. incomtus* are conspecific seems more plausible, but such a hypothesis needs to be carefully evaluated before accepting this nomenclatural action. Critical insight to the geographic limits and relationships of the two West African taxa will require taxonomic studies of other populations of *Dasymys*, particularly those in central and eastern Africa where some ten forms have been described, all of them now regarded as subspecies of *D. incomtus* (Ellerman 1941, Misonne 1974). Until such results are forthcoming, we here list the specimens examined under the appropriate specific designations available for populations within the West African region.

Taxonomic Summary

Dasymys rufulus Miller

Dasymys rufulus Miller, 1900:639 (type locality, Liberia, Mount Coffee; holotype, USNM 83844).—Allen, 1939:383.

Dasymys incomtus rufulus, Ellerman, 1941: 123.—Rosevear, 1965:311.—Misonne, 1974:19.—Happold, 1987:132.

Specimens examined.—DAHOMY: Diho, Central Region, 08°05'N, 02°31'E, 1 (USNM); Kétou, Eastern Region, 07°21'N, 02°37'E, 2 (USNM); Nikki, Borgou Region, 09°56'N, 03°13'E, 3 (USNM); Zizonkamé, Central Region, 07°55'N, 02°01'E, 2 (USNM). GHANA: Efeipo Krom, Western Region, 04°57'N, 01°52'W, 1 (USNM); Piri-si, Upper Region, 10°07'N, 02°27'W, 5 (USNM); Pulima, Upper Region, 10°51'N,

02°03'W, 50 (USNM). IVORY COAST: 20 km NW Dabou, 05°25'N, 04°33'W, 2 (AMNH); Kong, Upper Region, 09°09'N, 04°37'W, 10 (USNM); Sienso, 09°25'N, 07°31'W, 26 (USNM). LIBERIA: Du River, Firestone Camp No. 3, 1 (MCZ); Du River, Harbel, 1 (MCZ); Duside, 37 (AMNH); Mount Coffee, 06°30'N, 10°35'W, 6 (USNM, holotype and type series). NIGERIA: Agoleri, 1.5 mi E, 06°22'N, 06°52'E, 1 (USNM); Ashaka, 05°38'N, 06°24'E, 1 (USNM); Dada, Northern Region, 11°34'N, 04°29'E, 37 (USNM); Ibadan, University of Ife, 07°23'N, 03°54'E, 6 (USNM); Iella, 2 mi E Bahindi, Northern Region, 2 (USNM); Mada River, 3 mi E Gudi, Northern Region, 08°54'N, 08°17'E, 2 (USNM); Sokoto, 12 mi N, 1 (USNM); Tangaza, Northern Region, 1 (USNM); Tsanchaga, 8 mi E Bida, Northern Region, 2 (USNM); University of Lagos, Federal District, 7 (USNM); Zaria, 15 mi NW, 1 (USNM). SIERRA LEONE: Sainya, 5.2 mi (by road) W Outamba-Kilimi National Park, Northern Province, 09°48'N, 12°27'W, 1 (USNM); Yengema, 07°49'N, 12°27'W, 2 (USNM). TOGO: Dapongo, 10°52'N, 00°13'E, 1 (USNM); Ezimé, 07°29'N, 00°56'E, 1 (USNM); Padori, 10°13'N, 00°25'E, 11 (USNM); Pagola, 08°11'N, 00°58'E, 4 (USNM); Pewa, 09°17'N, 01°14'E, 1 (USNM). TOTAL = 227.

Dasymys foxi Thomas

Dasymys foxi Thomas, 1912:685 (type locality, Nigeria, Panyam, 4000 ft; holotype, BMNH 12.4.3.15).—Allen, 1939: 382.

Dasymys incomtus foxi, Ellerman, 1941: 122.—Rosevear, 1965:312.—Misonne, 1974:19.—Happold, 1987:132.

Specimens examined.—NIGERIA: 2 mi N Panyam, 09°27'N, 09°09'E, 3 (USNM); Panyam Fish Farm, Jos Plateau, 09°27'N, 09°12'E, 52 (USNM); Ugar Jabar, 2 mi N Jemaa, Jos Plateau, Northern Region,

09°31'N, 08°23'E, 4 (USNM). TOTAL = 59.

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Appendix 1.—Cranial and external dimensions (in mm) of selected samples of *Dasymys*.

Species and OTU	<i>n</i>	Mean	Range	<i>SD</i>
Occipitonasal Length				
<i>D. rufulus</i>				
Ghana (G3)	37	32.9	30.4–36.7	1.41
Ivory Coast (I2)	13	33.7	31.3–37.7	1.87
Liberia (L1)	5	34.8	32.9–35.8	1.13
Nigeria (N4)	24	34.2	32.5–36.2	1.08
<i>D. foxi</i>				
Nigeria (N10)	43	36.3	33.1–39.3	1.37
Zygomatic Breadth				
<i>D. rufulus</i>				
Ghana (G3)	37	17.9	16.7–19.1	0.67
Ivory Coast (I2)	15	17.5	16.3–17.5	0.77
Liberia (L1)	5	17.4	17.0–17.9	0.34
Nigeria (N4)	24	18.2	17.2–19.1	0.51
<i>D. foxi</i>				
Nigeria (N10)	43	19.2	18.1–20.1	0.53
Breadth of Braincase				
<i>D. rufulus</i>				
Ghana (G3)	37	13.4	12.9–14.3	0.31
Ivory Coast (I2)	15	13.4	12.8–14.4	0.44
Liberia (L1)	5	13.6	13.3–13.9	0.26
Nigeria (N4)	24	13.4	12.7–14.0	0.63
<i>D. foxi</i>				
Nigeria (N10)	43	14.1	13.6–15.0	0.34
Breadth across Exoccipital Condyles				
<i>D. rufulus</i>				
Ghana (G3)	37	7.33	6.7–7.7	0.22
Ivory Coast (I2)	15	7.52	7.2–8.0	0.21
Liberia (L1)	5	7.53	7.3–7.8	0.18
Nigeria (N4)	23	7.26	6.9–7.7	0.19
<i>D. foxi</i>				
Nigeria (N10)	41	7.94	7.6–8.3	0.19
Interorbital Breadth				
<i>D. rufulus</i>				
Ghana (G3)	37	4.40	4.0–4.8	0.16
Ivory Coast (I2)	15	4.33	4.1–4.7	0.13
Liberia (L1)	5	4.39	4.0–4.6	0.22
Nigeria (N4)	24	4.25	3.8–4.6	0.19
<i>D. foxi</i>				
Nigeria (N10)	43	4.51	4.2–4.9	0.15
Length of Rostrum				
<i>D. rufulus</i>				
Ghana (G3)	36	9.93	8.7–11.4	0.58
Ivory Coast (I2)	13	10.42	9.6–12.3	0.75
Liberia (L1)	5	11.04	10.5–11.3	0.31
Nigeria (N4)	24	10.61	9.8–11.3	0.38

Appendix 1.—Continued.

Species and OTU	<i>n</i>	Mean	Range	<i>SD</i>
<i>D. foxi</i>				
Nigeria (N10)	42	11.13	10.0–12.5	0.53
Postpalatal Length				
<i>D. rufulus</i>				
Ghana (G3)	37	12.03	10.9–14.2	0.72
Ivory Coast (I2)	14	11.90	10.8–13.5	0.82
Liberia (L1)	5	12.13	11.5–12.9	0.52
Nigeria (N4)	24	12.10	11.3–13.4	0.55
<i>D. foxi</i>				
Nigeria (N10)	41	13.08	11.3–14.9	0.73
Length of Bony Palate				
<i>D. rufulus</i>				
Ghana (G3)	37	6.72	5.7–7.3	0.33
Ivory Coast (I2)	14	6.77	6.0–7.6	0.42
Liberia (L1)	5	7.07	6.5–7.7	0.54
Nigeria (N4)	24	6.98	6.4–7.5	0.29
<i>D. foxi</i>				
Nigeria (N10)	42	7.25	6.7–7.9	0.31
Length of Diastemal Palate				
<i>D. rufulus</i>				
Ghana (G3)	37	9.96	8.9–11.7	0.58
Ivory Coast (I2)	15	9.77	8.9–11.2	0.69
Liberia (L1)	5	10.27	9.4–10.8	0.52
Nigeria (N4)	24	10.81	10.0–11.7	0.43
<i>D. foxi</i>				
Nigeria (N10)	43	11.32	10.1–12.5	0.56
Length of Incisive Foramina				
<i>D. rufulus</i>				
Ghana (G3)	37	7.48	6.6–8.4	0.44
Ivory Coast (I2)	15	7.45	6.6–8.4	0.56
Liberia (L1)	5	7.54	7.2–8.0	0.29
Nigeria (N4)	24	7.75	7.2–8.5	0.32
<i>D. foxi</i>				
Nigeria (N10)	43	8.14	7.5–9.2	0.40
Length of Auditory Bulla				
<i>D. rufulus</i>				
Ghana (G3)	37	5.33	5.1–5.5	0.17
Ivory Coast (I2)	15	5.21	4.9–5.5	0.19
Liberia (L1)	5	5.17	4.8–5.4	0.21
Nigeria (N4)	24	5.23	4.7–5.8	0.27
<i>D. foxi</i>				
Nigeria (N10)	42	5.75	5.2–6.1	0.20

Appendix 1.—Continued.

Species and OTU	<i>n</i>	Mean	Range	<i>SD</i>
Length of Maxillary Tooththrow				
<i>D. rufulus</i>				
Ghana (G3)	37	6.91	6.4–7.4	0.20
Ivory Coast (I2)	15	6.69	6.5–6.9	0.13
Liberia (L1)	5	6.76	6.6–7.0	0.14
Nigeria (N4)	24	6.61	6.2–7.1	0.23
<i>D. foxi</i>				
Nigeria (N10)	43	7.32	6.8–7.7	0.21
Width of M1				
<i>D. rufulus</i>				
Ghana (G3)	37	2.33	2.1–2.5	0.08
Ivory Coast (I2)	15	2.30	2.1–2.4	0.07
Liberia (L1)	5	2.28	2.2–2.3	0.02
Nigeria (N4)	24	2.21	2.0–2.3	0.06
<i>D. foxi</i>				
Nigeria (N10)	43	2.52	2.3–2.7	0.08
Total Length				
<i>D. rufulus</i>				
Ghana (G3)	49	260	222–313	18.8
Ivory Coast (I2)	25	281	239–324	26.5
Nigeria (N4)	34	280	254–322	17.7
<i>D. foxi</i>				
Nigeria (N10)	47	294	257–328	18.7
Tail Length				
<i>D. rufulus</i>				
Ghana (G3)	49	122	102–146	9.6
Ivory Coast (I2)	26	138	108–158	12.7
Nigeria (N4)	34	131	114–161	10.0
<i>D. foxi</i>				
Nigeria (N10)	46	136	121–155	8.7
Hindfoot Length				
<i>D. rufulus</i>				
Ghana (G3)	50	32.2	30–35	1.2
Ivory Coast (I2)	26	32.8	30–36	1.4
Nigeria (N4)	36	31.8	27–36	2.2
<i>D. foxi</i>				
Nigeria (N10)	49	33.6	31–37	1.3
Weight				
<i>D. rufulus</i>				
Ghana (G3)	50	76	45–125	16.0
Ivory Coast (I2)	26	77	44–116	19.6
Nigeria (N4)	36	82	61–116	14.9
<i>D. foxi</i>				
Nigeria (N10)	49	118	73–174	23.9